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► **To cite this version:**

Aline Peltier, Jean-François Ponge, Rafael Jordana, Arturo Ariño. Humus forms in Mediterranean scrublands with Aleppo pine. *Soil Science Society of America Journal*, 2001, 65 (3), pp.884-896. 10.2136/sssaj2001.653884x . hal-00501849

HAL Id: hal-00501849

<https://hal.science/hal-00501849>

Submitted on 12 Jul 2010

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DIVISION S-7—FOREST & RANGE SOILS

Humus Forms in Mediterranean Scrublands with Aleppo Pine

Aline Peltier, Jean-François Ponge,* Rafael Jordana, and Arturo Ariño

ABSTRACT

Commonly reported effects of pine on topsoil include acidification, a decrease in biological activity, and an accumulation of surface organic matter. Such effects have not been documented for Mediterranean woodland and scrubland areas. This research evaluated humus profiles beneath pine and adjacent vegetation on the basis of previous knowledge on soil animal communities and vegetation. Two Mediterranean sites with aleppo pine (*Pinus halepensis* P. Mill.) and scrubland vegetation were compared, one in Spain (Navarre), the other in Italy (Sicily). Humus profiles were sampled under main vegetation types, comprising aleppo pine, rosemary (*Rosmarinus officinalis* L.), and bare ground in both sites, along transects with increasing pine influence. Quantitative morphological methods were used to analyze and compare humus profiles, and data were analyzed using correspondence analysis. In both sites the influence of aleppo pine on humus forms was well-defined but minor, increasing the appearance of an Oe horizon characterized by intense activity of litter-dwelling fauna and fungi. Under all vegetation types, and in both sites, the organomineral A horizon was of the mull type, although the composition of the soil-building fauna varied between Navarre and Sicily. There was more heterogeneity among vegetation types in Navarre, where aleppo pine was planted on derelict land, than in Sicily where aleppo pine was a component of natural vegetation (maquis). A decreasing influence of pine was perceptible in the inner edge of the pine plantation in Navarre, or under the crown of individual trees in Sicily.

THE INFLUENCE OF PINE on soils and soil biological processes has been the subject of numerous studies. Most studies have compared pine with broad-leaved species living in nearby stands (Hamilton, 1965; Arpin et al., 1986a, 1986b) or in the understory (Tappeiner and Alm, 1975; Ponge and Prat, 1982) or along successions (Fisher, 1928; McClurkin, 1970). Aleppo pine is quite common in landscapes surrounding the Mediterranean sea, either naturally established or planted. It lives together with other members of evergreen shrubby vegetation, such as rosemary, kermes oak (*Quercus coccifera* L.), and pistachio (*Pistacia lentiscus* L.), forming what is commonly called maquis (Gindel, 1964; Poli Marchese et al., 1988). Overgrazing as well as recurrent fires may locally affect these ecosystems to the point that they turn to derelict land (Naveh, 1971; Pons and Thinin, 1987). Commonly reported effects of pine on the topsoil,

such as acidification (Ovington, 1953; Zinke, 1962; Riha et al., 1986), accumulation of organic matter (Ovington, 1954; Van Berghem et al., 1986), cation leaching (Bloomfield, 1953), and decrease in biological activity (Bauzon et al., 1969), are mainly due to the richness of pine litter (bark included) in terpenic and phenolic compounds (Berg et al., 1980; Kuiters, 1990), and to the recalcitrant nature (both mechanical and biochemical) of its needle litter (Berg and Wessén, 1984; Reh et al., 1990). Other (indirect) effects have been suspected, notably through the development of a dense lichen, moss, fern, grass, or ericaceous layer in the understory (Robinson, 1972; Berg, 1984; Lawrey, 1986). We may wonder whether similar effects are present in Mediterranean landscapes, which include pines and oaks, as well as numerous woody legumes. Bare ground is also a common feature of these open landscapes and could be compared with zones where aleppo pine has been used for afforestation and soil restoration.

Previous studies (Bernier and Ponge, 1994; Ponge and Delhay, 1995; Bernier, 1996; Ponge et al., 1997; Bernier, 1998; Ponge, 1999) have shown that the interplay between plant and soil animal communities was reflected in the composition of humus profiles. In particular, the analysis of humus profiles by laboratory optical methods can inform us about the dynamic state of the ecosystem (Ponge et al., 1998) and the level of soil biodiversity (Ponge et al., 1997). In this study we applied these methods to an assessment of the effects of aleppo pine on soil biological activity in Mediterranean landscapes where pine occurs either as a component of unmanaged vegetation or is planted in monoculture for site reclamation.

MATERIAL AND METHODS

Study Sites

This study was conducted in two aleppo pine-dominated sites under Mediterranean climate. One site is a now derelict, formerly overgrazed land recently planted in pine. The other site contains pine as a natural component of an old-growth maquis vegetation. We studied the composition of topsoil horizons (humus profiles) under different vegetation types, using optical methods devised for forest soils by Bernier and Ponge (1994) and Ponge (1999). These methods allow the identification of most biological components of the ectorganic as well as the hemorganic horizons. Ecolines (Van der Maarel, 1990) between aleppo pine and other vegetation were emphasized in our sampling procedure, in order to follow changes in humus profiles under the increasing influence of pine, including possible edge effects (Harris, 1988).

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The first site was located in the southern part of Navarre, Spain, near the village of Funes, close to the Bardenas area. This strongly eroded agricultural land had been overgrazed for centuries. Reafforestation programs were started 30 to 40 yr ago in order to create islands of soil restoration. Aleppo pine was planted at a high density and these stands had not been thinned at the time of our study. Average tree height was 7.5 m. Some young isolated pine trees established themselves in the scrubland surrounding the plantations, thus forming a transition zone (outer edge) between the scattered, still grazed, scrubland and the plantation. Within the boundary of the plantation we distinguished another transition zone (inner edge), where ground vegetation was more abundant. The geological substrate was gypsum. Soils were Haploxerepts, with little accumulated litter, except under pine where a continuous layer of needles was visible on the ground. Climate was of the Mediterranean type, fairly warm and dry (mean annual temperature 14°C, mean annual rainfall 419 mm), with moderate winter. The study site was located on a slope (13%) at 470 m above sea level, with a north-northeast aspect. The scrubland was dominated by rosemary and thyme (*Thymus vulgaris* L.). In the plantation false brome [*Brachypodium ramosum* (L.) R. & S.] dominated the understory. In the inner edge scrubland species were also present in mixture.

The second site was located in southeastern Sicily, in the Ippari River Valley, near Vittoria Veneta. Aleppo pine was dominant in patches of undisturbed scrubland, with rosemary and pistachio as accompanying species, which are remnants of the climax vegetation that once covered Sicily. The surrounding landscape is mainly composed of orange (*Citrus reticulata* L.) groves. The time interval between recurrent fires affecting the scrubland is ≈ 70 yr, and this was the age of most dominant individuals of aleppo pine. Aleppo pine, rosemary, and pistachio were growing isolated, except in the periphery of pine crowns where branches of pistachio were growing in the understory. It appears that after fire aleppo pine is the first vegetation to become established and gaps are filled thereafter by other scrubland species. We considered that ecoclines were present under the crown of each individual pine (mean height 9 m), from the trunk base to the crown border, where there was an admixture of other scrubland species. Small areas not covered with vegetation were present (1% of total surface), but in these areas the ground was still covered with pine litter. The herb layer was practically absent. Pine pollen was especially abundant in the litter, because of intense flowering. The geological substrate was gypsum. Soils were Haploxerepts with more accumulated litter than in the Navarre site, especially under the pine and the pistachio. The slope was 16%, with a northwest aspect. Climate was of the warm Mediterranean type, with a short rainy period in winter and a long warm dry period from May to September.

Sampling Design

In the Navarre site, five transect lines about 90 m long and 2 m wide were established that crossed the southeastern side of the plantation at 10-m intervals. These transects ran from the overgrazed scrubland (outer edge) to the interior of the plantation (farthest point from all edges of the plantation). Only three of the five transect lines were used for sampling humus profiles. Along each transect line the topsoil was sampled under seven vegetation types, including both the overgrazed scrubland and the pine plantation as follows:

Pine plantation (inside of the plantation, without any admixture of scrubland vegetation)

Inner edge 1 (most internal part of the inner edge, showing first signs of admixture)
 Inner edge 2 (midpart of the inner edge)
 Inner edge 3 (most external part of the inner edge, under the crown of most external trees)
 Isolated pine (outer edge, scrubland)
 Bare ground (outer edge, areas not covered with scrubland vegetation)
 Rosemary (outer edge, scrubland)

Care was taken to collect samples under these well-defined cover types rather than at fixed intervals.

In the Sicily site, three transect lines about 7 m long were established under three adjoining pine trees, converging towards a central area occupied by other scrubland species or bare ground. The sampling was replicated three times in the central area. The seven vegetation types sampled (three samples each) were

Pine 1 (near the trunk base)
 Pine 2 (at mid distance between the trunk base and the crown border)
 Pine 3 (at mid distance between Pine 2 and the crown border)
 Pine 4 (just at the crown border)
 Pistachio (central area)
 Bare ground (central area)
 Rosemary (central area)

Sampling was completed in November 1994 at the Navarre site and in December 1994 at the Sicily site. A total of 42 soil samples (21 in Navarre, 21 in Sicily) were collected.

Sampling Procedure

Soil cores were collected using a specially built steel and aluminum corer (Fig. 1). It included an external jacket and an internal sleeve, thus resembling the corer devised by Macfadyen (1962). However, it had a 45 by 45 mm square section and the cutting edge was not the jacket, but rather a discardable section of the internal sleeve, which had been slanted at 45° and sharpened. The jacket and the cutting portion of the sleeve were made from standard square steel profile. The jacket had a foot pad of steel soldered to the bottom. The sleeve consisted of a range of several seamless square, open aluminum boxes of equal size, made from standard square aluminum profile, prolonged distally by the steel cutting edge and proximally by a piston made of reinforced steel. The sleeve glided freely inside the jacket on soldered steel rails. The train made of the cutter and of the desired number of boxes (each 25 mm deep) was inserted at the bottom of the corer, then forced vertically into the soil with the piston, the reinforced top of which was hammered when necessary. The sampling depth was variable (according to stoniness of the soil), ranging from 40 mm (two boxes) to 100 mm (five boxes).

After withdrawing the jacket, the train of boxes was recovered and the soil core was cut between the boxes by means of a wide-blade sharp knife. Top and bottom were marked; then each box was labeled and covered on both sides by aluminum lids secured by rubber bands. The boxes were then placed into plastic containers filled with 4% formalin, sealed, and transported to the laboratory. Afterwards they were transferred to water, then to 75% ethyl alcohol. The boxes remained closed during all these procedures, in order to disturb soil and faunal material as little as possible. Liquids seeped in and out freely through tiny interstices between boxes and lids.

For transportation to the French laboratory, where analysis of the soil matrix took place, alcohol was allowed to seep out

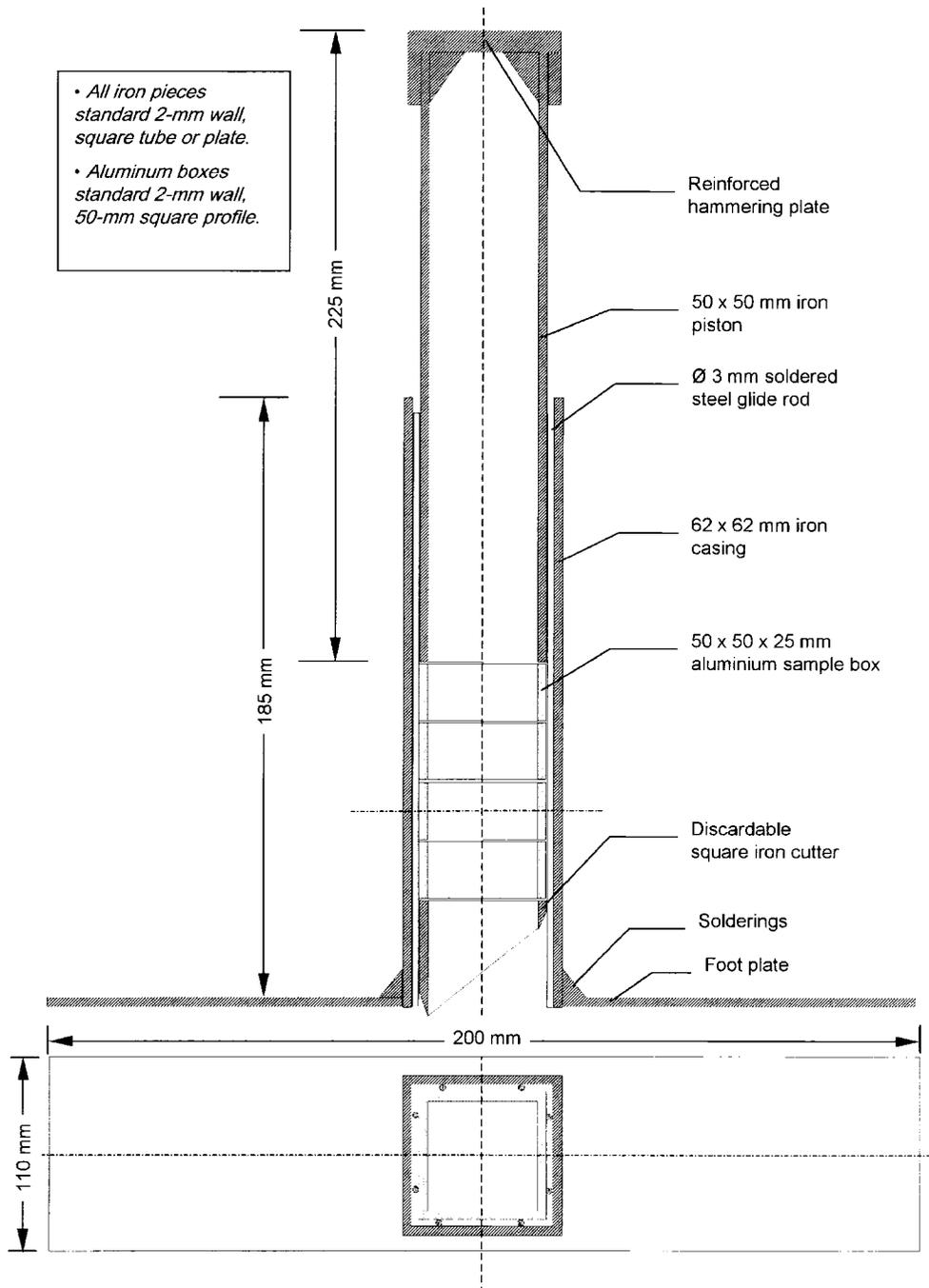


Fig. 1. The sample corer used to collect soil horizons.

of the boxes, but drying of the samples was avoided by putting each box in a sealed bag with an alcohol-impregnated cotton swab. Sets of sealed samples were then placed in air-tight containers for transportation and storage until analysis.

Morphological Analysis

The boxes filled with litter and soil material were gently immersed into 95% ethyl alcohol. Then the upper surface was observed under a dissecting microscope. Soil and litter components were sorted into categories, taking into account their origin (plant, animal, microbial, mineral, and mixed) and

their stage of decomposition or weathering. Following the technique by Ponge (1984) modified by Bernier and Ponge (1994), a piece of counting glass etched with a regular 200-point grid was placed at the top of each box, and the number of points that covered each category was counted. This procedure allowed determination of the percentage in volume of each category at a given depth level. Afterwards, the material contained in the boxes was progressively excavated with tweezers down to a new horizon, if any. Then a new set of observations was completed. Successive observations were used to follow changes in the composition of the soil matrix along a given profile. When necessary for calculations, the composition pre-

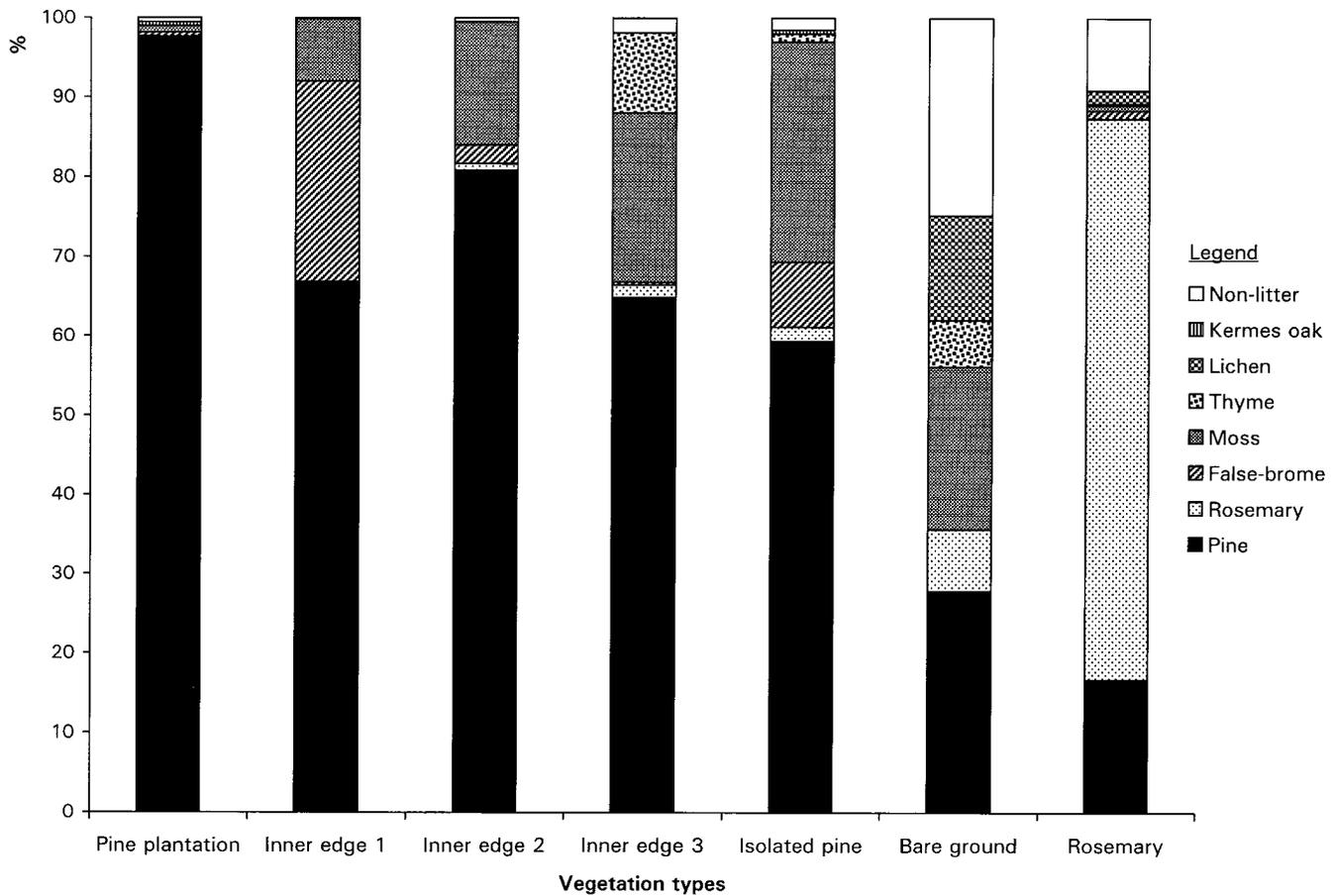


Fig. 2. Composition of litter in Navarre as indicated by surface countings.

vailing at a given depth level was estimated by interpolation between observations immediately above and below the level.

Statistical Analysis

Data (percentages of occurrence of different categories at different depth levels in different humus profiles) were analyzed by simple correspondence analysis, a multivariate method using the chi-square distance (Greenacre, 1984). This graphical data exploratory technique has been previously applied to the analysis of sets of humus profiles by Ponge (1999). It allows classification of horizons as well as successions of horizons (humus profiles) on the basis of the composition of the soil matrix. Active variables or rows (variables from which characteristic roots of the covariance matrix were derived) were the percentages of occurrence of the categories. They were standardized according to Ponge and Delhaye (1995), by arbitrarily fixing the mean to 20 and the variance to one. In this way, factorial coordinates of the variables along a given axis were interpreted in terms of their contribution to this axis; that is, the farther a point is from the origin (barycenter) along an axis, the more it has contributed to the formation of the axis and, thus, the more weight it should be given when interpreting the axis. Observations (columns) were the different counts, which were done over the whole set of humus profiles. Thus, each count was assigned both to a given depth level and to a given humus profile. As this is possible in correspondence analysis, rows (variables) and columns (observations) were projected together on planes made of combina-

tions of the first factorial axes (those corresponding to the highest eigenvalues), thus describing by a geometrical model global patterns emerging from the data matrix. Departure of the first factorial axes from random partitioning of the total variance was tested using the procedure of Lebart et al. (1979).

Passive (additional) variables were used to facilitate interpretation of the factorial axes and to make charts easier to evaluate. In order to assess the influence of depth on the composition of humus profiles, depth levels (cm) were added to the data matrix, without contributing to the formation of factorial axes. They were projected on the factorial axes, taking into account their distance to the counts. Each depth level (each centimeter) was considered as a distinct variable. Fuzzy coding (0.x) was used when a given count was made between two successive centimeters, otherwise depth levels were coded as 1 or 0. Vegetational types and horizons were also used as passive variables, following the same procedure. In correspondence analysis all points corresponding with rows (active and passive variables) and columns (counts) can be projected as points on the same factorial axes. This property facilitates interpretation. If we want to know whether a humus component is (on average) associated with a given depth level or with a given vegetation type, we need only to search for those depth level indicators (centimeters) and those vegetation types that are projected in its vicinity. In our analyses, only passive and active variables were projected on factorial axes, since we did not need information about individual counts. Rather, we desired a synthetic view of changes with depth and changes among vegetation types.

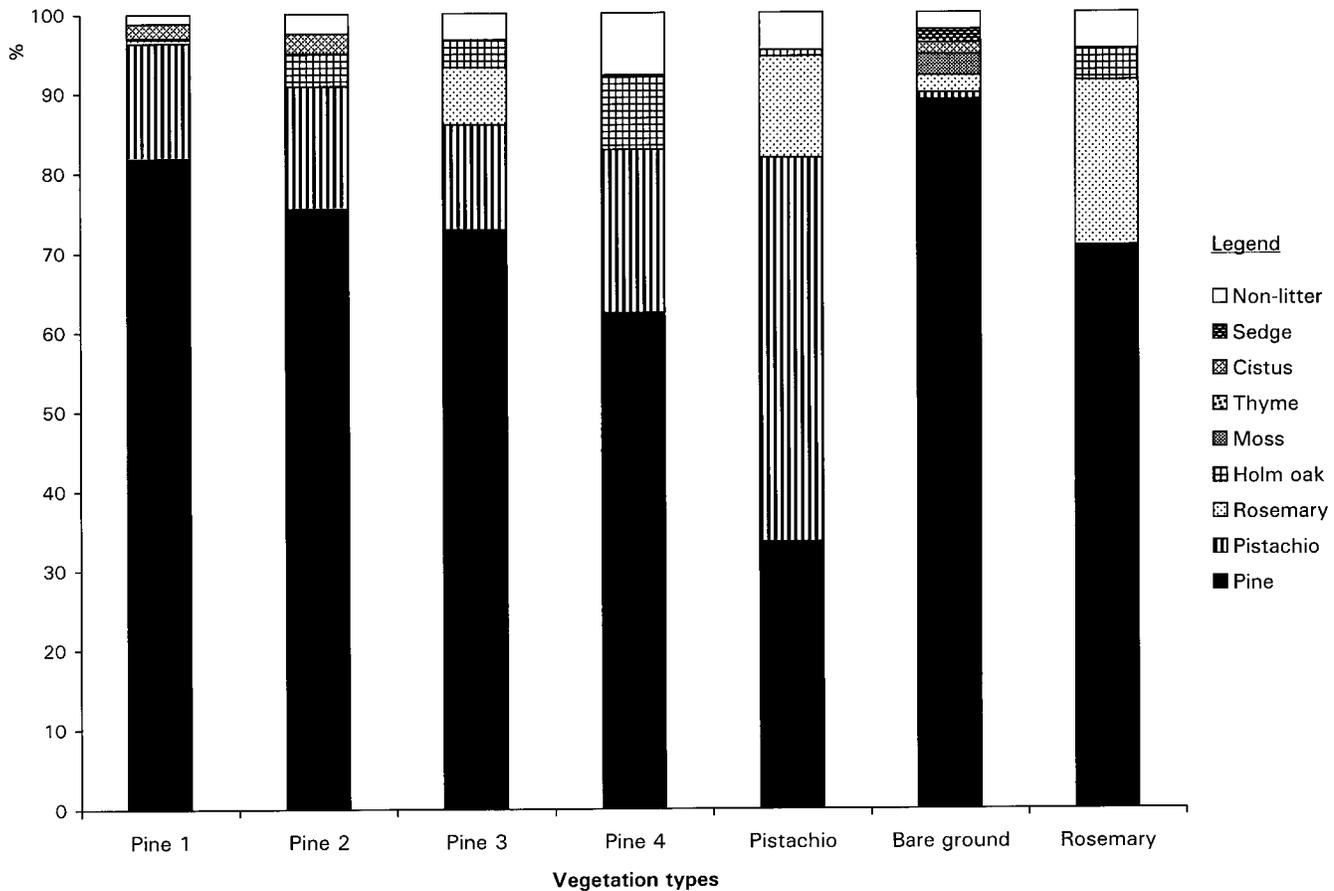


Fig. 3. Composition of litter in Sicily as indicated by surface countings.

RESULTS

Classification of Humus Components into Categories

One hundred sixty-six categories were identified (Table 1). Differences between sites were mostly due to differences in the composition of vegetation; for example, pistachio, cistus (*Cistus* spp.), and holm oak (*Quercus ilex* L.) were absent from the Navarran site and false-brome and thyme were absent from the Sicilian site.

Litter Composition

Surface counts provided a picture of the composition of recently fallen litter, which could be compared between sites and among vegetation types.

In Navarre (Fig. 2), pine components comprised more than one-half of the litter only under pine, whether planted or disseminated in the scrubland. Within the interior of the plantation they comprised the bulk of surface litter, while in the inner edge and under isolated pines they comprised only from 60 to 80% of total litter and 15 to 30% only in the rest of the scrubland, significantly less than in the plantation. Under rosemary (the most typical vegetation of the overgrazed scrubland) the litter comprised 10% of non-plant components (animal feces, roots, mineral soil). In bare areas non-plant litter components comprised 25% of total counts (significantly more than in other vegetational types, except

rosemary), while the remaining counts consisted of a mix of pine, moss, lichen, rosemary, and thyme litter, in decreasing order. The importance of lichens covering bare areas should be emphasized, as this vegetation was often invisible to the naked eye. The composition of litter in the inner edge was characterized by greater amounts of false-brome litter than other vegetation types. An increase in moss litter was perceptible from the inside to the edge of the pine plantation and then to isolated pines, but strong variations in moss cover from one sampling point to another made the response of this vegetation to environmental influences rather erratic.

In Sicily (Fig. 3), pine litter was abundant under all vegetation types, but it was most abundant on bare ground (90% of total components). The fact that areas without any vegetation were covered by pine litter and that plant litter components other than pine were present even near pine trunks was a major trait of high maquis in Sicily compared with derelict scrubland in Navarre. A small decrease in the contribution of pine to litter, paralleled by an increase in pistachio litter, was perceptible in the gradient from Pine 1 (near the trunk) to Pine 4 (crown edge).

Humus Profiles

Correspondence analysis was performed on all counts done in Navarre. Axes 1 and 2 extracted 6.5 and 5.7%

Table 1. List of humus components (categories).

Number	Location†	Condition‡	Description
1	NS		bark-free pine wood
2	NS		pine twig
2b	NS		pine branch
3	NS		orange entire pine needle
4	NS		brown entire pine needle
4b	NS		brown entire pine needle + white mycelium
5	N		false brome stem
6	N		false brome leaf
7	NS		thin pine bark fragment
7f	NS		pine female cone scale
8	NS		entire pine short shoot
8m	N		entire pine short shoot + mineral particles
8b	S		entire pine short shoot + white mycelium
8*	NS	F	nibbled pine short shoot
9a	NS	OM	round-shaped organo-mineral fecal pellet > 0,5 mm
9b	NS	OM	round-shaped organo-mineral fecal pellet < 0,5 mm
10	N		kermes oak leaf
12	NS		pine male flower scale
12b	NS		pine male flower scale + mineral particles
12m	NS		pine male flower scale + white mycelium
13	NS		living moss
13*	NS		dead moss
13g	N		nibbled dead moss
14	NS		arthropod body
15	NS	F	fragmented brown pine needle
15b	NS	F	fragmented brown pine needle + white mycelium
16	NS	F	fragmented brown pine needle + mineral particles or black mycelium
17	NS		miscellaneous
18	N		thyme stem <3 mm
18g	N	F	nibbled thyme stem
19	N		thyme leaf
19*	N		dead thyme leaf
19g	N	F	nibbled thyme leaf
20	NS		mineral particles <0.5 mm
21	NS		thyme seedling
22	N		lichen-covered pine branch
25	NS		lichen alone
26	NS		entire orange rosemary leaf
27	NS		entire brown rosemary leaf
28	NS		rosemary stem <3 mm
28*	NS	F	nibbled rosemary stem
29	NS	F	fragmented rosemary leaf
29*	NS	F	fragmented and nibbled rosemary leaf
30	NS		rosemary fruit base
30*	NS		broken rosemary fruit base
31	N	F	fragmented false brome stem
31*	N	F	fragmented and nibbled false brome stem
32	NS		mineral particles (0,5-3 mm)
33	NS		mineral particles >3 mm
34	NS		organic fecal pellet (earthworm)
35	NS		pine euphyll
35m	NS		mineral-encrusted pine euphyll
35f	NS	F	fragmented pine euphyll
36	NS		thick pine bark fragment
37	NS		rosemary branch >3 mm
37*	NS	F	nibbled rosemary branch
38	N		lichen-covered moss
39	N		brown hyphae on old fecal pellets
40	N		moss-covered pine bark
41	NS		lichen-covered pine bark
42	N		pine bark covered with mineral particles
43	N		pine bark covered with dead moss
44	N		rosemary seedling
46	NS		thyme fruit
47	N		lichen-covered rosemary stem
48	NS		mass of melanized mycelium
50	NS	F	food remains (wood or scales)
51	NS		organo-mineral mass
52	NS		holorganic feces of insect larvae
53	NS	F	pine male cone, nibbled and cut off
53m	NS	F	nibbled pine male cone covered with mineral particles
54	NS		dead pine fine root
55	NS		rosemary achene
56	NS		living pine fine root
57	N		rosemary or thyme flower remain
58	NS		pine large root
59	NS	F	nibbled and decayed wood
60	NS	F	fragmented and nibbled pine needle
60b	S	F	nibbled pine needle covered with white mycelium
60*	NS	F	finely fragmented pine needle
61	NS	F	food remains covered with mineral particles
62	S		brown entire pistachio leaflet

Continued.

Table 1. Continued.

Number	Location†	Condition‡	Description
63	NS		pistachio twig <3 mm
64	NS		billet-like hologanic fecal pellet
65	NS		mass of white mycelium
66	NS		entire snail shell
66*	NS		fragmented snail shell
67	S	F	fragmented pistachio petiole or rachis
68	NS		hologanic millipede fecal pellet
69	NS		whitish and brittle mineral particles
70	S	F	fragmented brown pistachio leaflet
70m	S	F	fragmented pistachio leaflet covered with mineral particles
70*	S	F	finely fragmented pistachio leaflet
71	NS		woodlouse hologanic fecal pellet
72	NS		faunal-modified old fecal pellet
73	S		pistachio large root
73*	S		nibbled pistachio large root
74	S		pistachio fine root
74*	S		nibbled pistachio fine root
75	S	OM	coarse-grained organo-mineral fecal pellet
76	S		cistus large root
77	S		hologanic millipede fecal pellet made of pollen grains
78	NS		hologanic mite fecal pellet
79	NS		unidentified organic fecal pellet made of coarse particles
80	S		entire brown cistus leaf
81	S	F	nibbled pistachio rachis
82	S		entire spiny holm oak leaf
83	S		cistus fine root
84	N		false brome fine root
84*	N		dead false brome fine root
85	N		false brome large root
86	NS	OM	organo-mineral fecal pellet without definite shape
87	S		cistus seedling
88	S		pine seed wing
89	NS		white rhizomorph
90	S		intact pistachio rachis
91	S	F	fragmented cistus leaf
92	S	F	fragmented holm oak acorn
93	S		cistus twig
94	NS		piece of charcoal
95	NS		pine pollen grains
96	S		undetermined grass
97	NS		pine bud
98	S		inflorescence of undetermined grass
99	S		root of undetermined grass
100	NS		gypsum particles >3 mm
101	N		gypsum particles (0.5–3 mm)
102	NS		yellow-light orange rhizomorph
103	N		very young rosemary seedling
104	NS		rosemary large root
105	NS		rosemary fine root
106	S		pistachio seedling
107	S		pine seedling
108	S		piece of undetermined seedling
109	S		earthworm
110	S		unlignified seedling root of undetermined plant species
111	S		pistachio bark
112	S		brown-red smooth holm oak leaf
112*	S		fragmented smooth holm oak leaf
113	N		thyme branch >3 mm
114	N		thyme branch + lichen
115	N	F	fragmented thyme leaf
116	N	F	fragmented thyme stem
117	N		thyme fine root
117*	N		fragmented thyme fine root
118	N		thyme large root
119	N		flat seed, oval-round, black >3 mm
120	S		holm oak twig <3 mm
121	S	F	fragmented holm oak branch >3 mm
122	S		wild madder leaf
123	S		wild madder stem
124	S		undetermined spiny herb shoot
125	S		undetermined subterranean grass stem
126	S		holm oak large root
127	S		holm oak fine root
128	S		pistachio branch >3 mm
129	S		lichen-covered pine needle
130	S		piece of lava
131	N		black lichen with green hairs
132	N		moss sporogonium cap
133	NS		thick-walled long rhizoids
134	S		sedge leaf

† N = Navarra, S = Sicilia.

‡ F = faunal-conditioned litter, OM = organo-mineral fecal material.

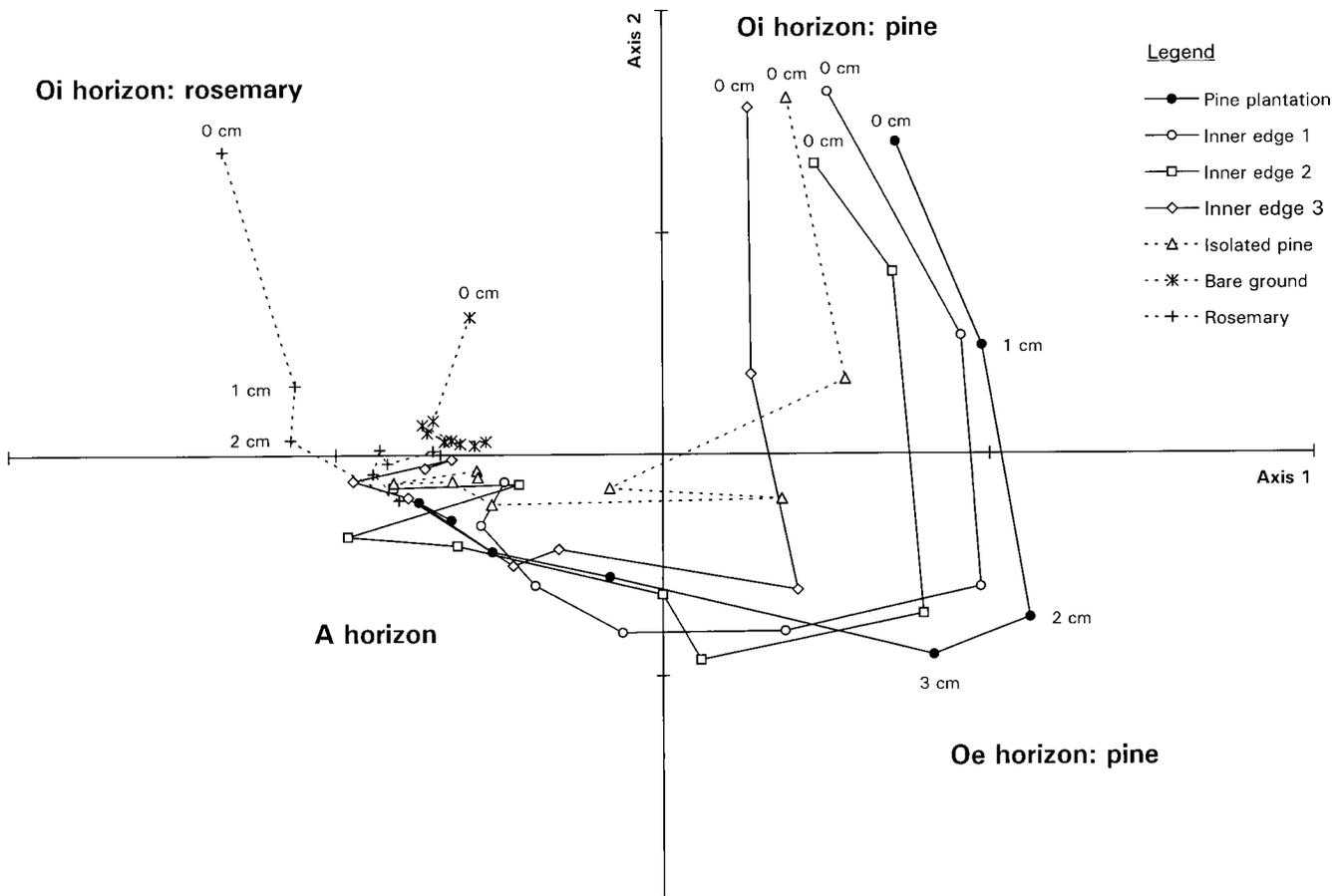


Fig. 5. Correspondence analysis of Navarran humus profiles. Projection of passive variables (depth levels) in the plane of the first two axes.

Edge effects were visible in the pine plantation. There was a progressive shift in the composition of the Oi horizon and in the passage to a typical Oe horizon, both becoming less and less distinct as far as the edge of the plantation was reached. Isolated pines exhibited features similar to the inner edge of the pine plantation.

Some categories of humus components were pooled in order to compare vegetation types in Navarre, using 2 and 4 cm as reference depths, for Oe horizon (under pine) and A horizons (under all vegetation types), respectively. Organo-mineral fecal material (typical of A horizon) comprised four categories, and faunal-conditioned litter (typical of Oe horizon) comprised 31 categories (Table 1). Both pooled categories exhibited a variation according to vegetation at the 2-cm depth. Organo-mineral feces were more abundant under rosemary (21.5%) than at the inside of the pine plantation (1.7%), other vegetation types being intermediary. Faunal-conditioned litter was more abundant under pine (31–66%) than under rosemary (19%) or on bare ground (1.5%). In contrast, at the 4-cm depth variations between vegetation types were negligible for both organo-mineral fecal material and faunal-conditioned litter.

In Sicily, Axes 1 and 2 of correspondence analysis extracted 6.3 and 5.1% of the total variance, which indicated a significant departure from random according to the number of rows and columns of the data matrix

(126 categories and 155 counts, respectively). The projection of humus components in the plane of Axes 1 and 2 of correspondence analysis (Fig. 5) indicated three different kinds of composition, corresponding with Oi, Oe, and A horizons, whatever the vegetation type. Oi horizons were characterized by orange entire pine needles (3), brown entire pine needles (4), entire pine short shoots (8), pine seed wings (88), brown entire pistachio leaflets (62), rosemary stems <3 mm (28), entire orange rosemary leaves (26), and undetermined grasses (96). Oe horizons were characterized by fragmented and nibbled pine needles (60), fragmented brown pine needles (15), nibbled and cut off pine male cones (53), fragmented brown pistachio leaflets (70), holorganic millipede fecal pellets made of pollen grains (77), holorganic millipede fecal pellets (68), food remains made of wood and scales (50), holorganic mite fecal pellets (78), and faunal-modified old fecal pellets (72). A horizons were characterized by mineral particles <0.5 mm (20), fragmented snail shells (66*), organo-mineral fecal pellets without definite shape (86), and coarse-grained organo-mineral fecal pellets (75).

Depth trajectories in Sicily (Fig. 6 and Fig. 7) indicated some shifts in the passage from Oi to Oe then to A horizons from one vegetation type to another. Under a pine crown, the appearance of a distinct Oe horizon was less pronounced as distance from the trunk base increased (i.e., along the sequence Pine 1, Pine 2, Pine

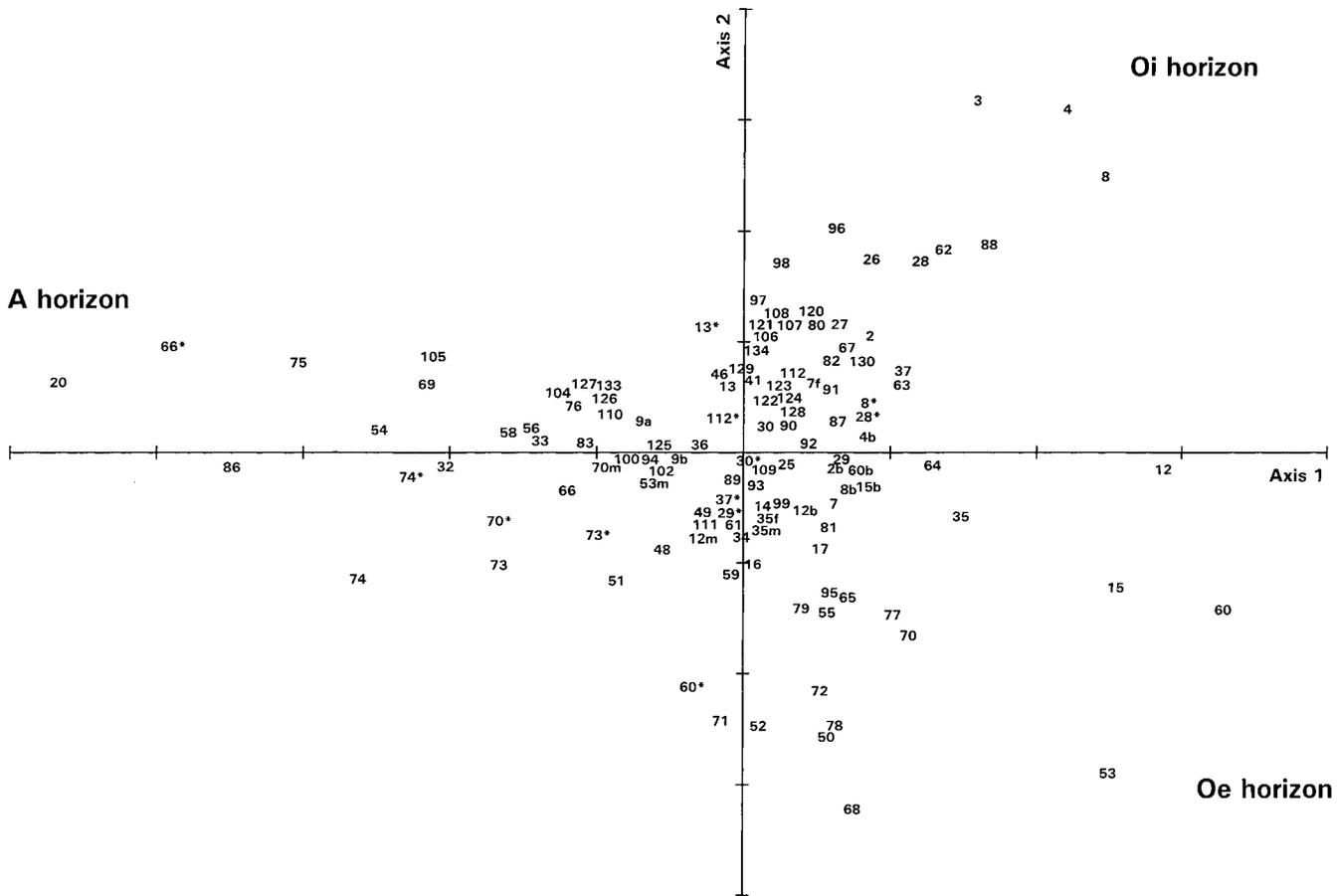


Fig. 6. Correspondence analysis of Sicilian humus profiles. Projection of active variables (humus components) in the plane of the first two axes.

3, Pine 4). Trajectories under rosemary and pistachio were not very different from what could be observed under the peripheral half of pine crowns (Pine 2 to Pine 4). Bare ground exhibited the more direct passage from the Oi to A horizon, despite the abundance of pine litter at the ground surface (Fig. 2).

Differences between the two studied sites were mostly expressed in the composition of the Oi horizon, which did not differ as greatly among vegetation types in Sicily as in Navarre, in the appearance of an Oe horizon under rosemary in Sicily but not in Navarre, and in the composition of the A horizon, which did not exhibit the same organo-mineral feces. All organo-mineral fecal pellets were round-shaped in Navarre (93% > 5 mm, 7% < 5 mm), while these categories were nearly absent from Sicily. In Sicily, they were replaced by feces of indefinite shape (92%) or coarse-grained (8%). In Navarre, repeated application of dilute formaline along all transect lines revealed the presence of only one species, the large endogeic earthworm *Scherotheca campoii* Lainez and Jordana 1987, under all vegetation types. This species, native to Navarre (Lainez and Jordana, 1987), was thought to be responsible for the presence of round-shaped organo-mineral aggregates within the A horizon. Examination of gut contents of collected individuals revealed the dominance of organo-mineral material mixed with pine needles (11%) and roots (14%) under pine, or with rosemary aerial (9%) and subterranean

parts (11%) under rosemary. In Sicily, such extraction was not done, given the absence of visible earthworm activity, but ocular field observation revealed the presence of numerous tenebrionid beetle larvae and adults burrowing into the A horizon.

DISCUSSION

The method we used for studying the micromorphology of humus profiles is inexpensive and reliable and allows for quantitative (Bernier and Ponge, 1994; Bernier, 1996, 1998) or semiquantitative (Ponge, 1999) analysis of the composition of the soil matrix. Nevertheless, it cannot replace observation of soil sections (Zachariae, 1965; Bal, 1970; Babel, 1975) when data on the distribution of cavities and burrows are sought. Combined with the use of multivariate methods, it can aid comparisons among horizons and humus profiles.

All humus profiles studied are characterized by a crumbly A horizon mainly made of organo-mineral fecal pellets and sand particles. In the hemorganic part of the humus profile, differences between Navarre and Sicily are related to the animal origin of hemorganic feces, which are seemingly produced by earthworms in Navarre and by insects in Sicily. Mull is the dominant humus form in both sites and under every vegetation type. Under aleppo pine, either planted or naturally established, there is an accumulation of fragmented pine

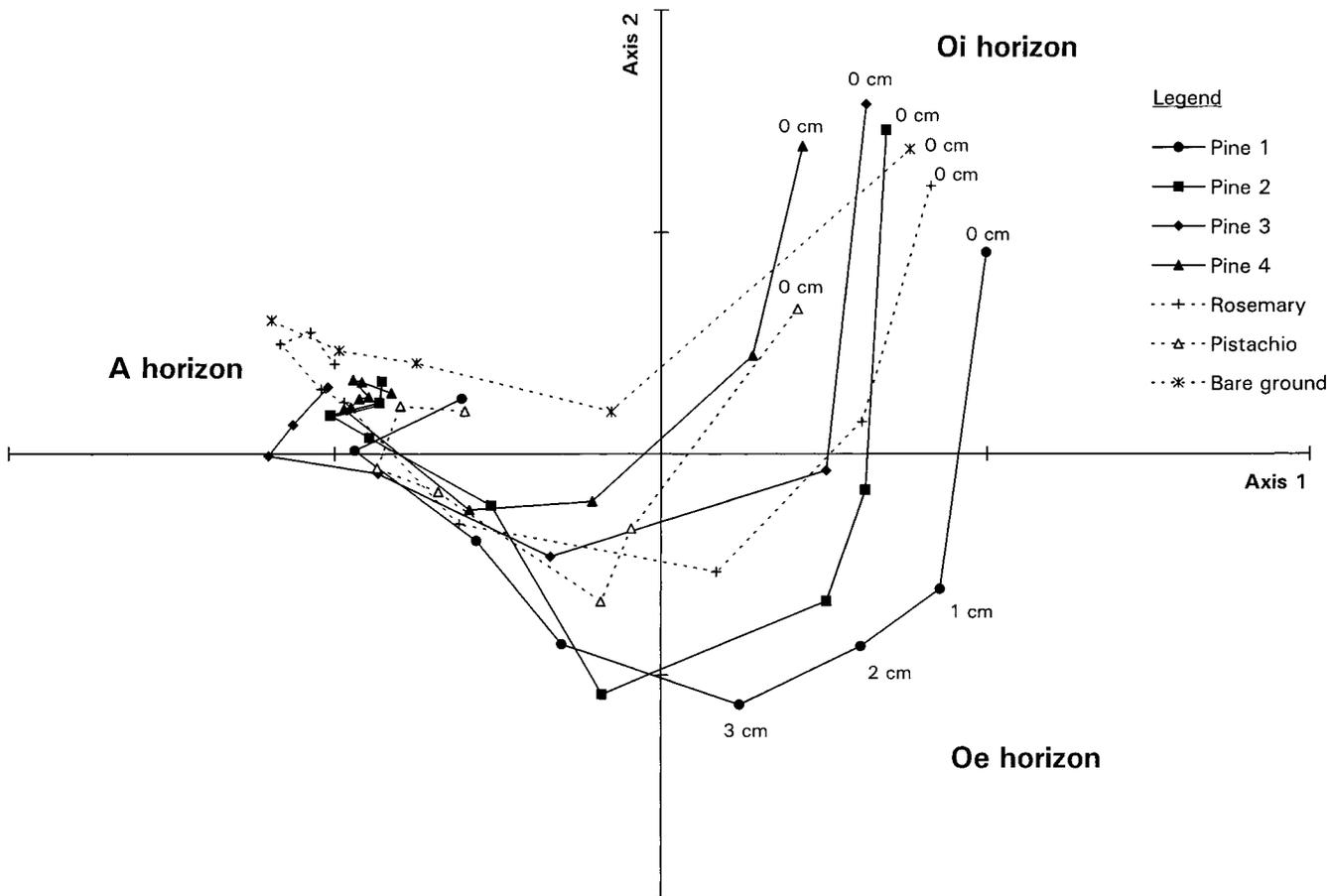


Fig. 7. Correspondence analysis of Sicilian humus profiles. Projection of passive variables (depth levels) in the plane of the first two axes.

litter, mixed with holorganic feces of epigeic fauna (mainly mites and millipedes) at the top of the mull profile (Oe horizon). In Sicily, the Oe horizon is visible under pistachio and rosemary as well (Fig. 6). All studied humus profiles exhibit a crumbly hemorganic A horizon; thus the humus form is mull. However strong variations have been observed in the development of the Oe horizon. Brêthes et al. (1995) described a variety of humus forms belonging to the mull group, from eumull (mull with a thin Oi horizon and absence of Oe horizon) to amphimull (mull with Oi, Oe, and Oa horizons). Mesomull (Oi and thin Oe) and dysmull (Oi and thick Oe) are intermediary. In our sample the humus form varies from eumull, under rosemary and bare ground in Navarre, to dysmull, under pine in Navarre and under all vegetation types in Sicily. Thus, in our study sites, the influence of pine is minor compared with what is commonly reported in the literature, where moder or even mor humus forms are commonly observed under pine trees (Kendrick and Burges, 1962; Bal, 1970; Mettievier Meyer et al., 1986). Changes from mull to moder often follow establishment of softwood species in forests previously occupied by hardwoods (Bonneau, 1978; Arpin et al., 1986a). Reasons for such discrepancies are probably due to the milder climate and more base-rich substrate common in the south of Europe relative to northern countries (Elmi and Babin, 1996). Mull has been associated with an increase in biodiversity under

warmer climatic and richer trophic conditions (Ponge and Bernier, 1995; Bernier, 1996; Ponge et al., 1997). It cannot be excluded that an excessive development of some soil organisms typical of soils with a strong accumulation of organic matter, such as the enchytraeid *Cognettia sphagnetorum* (Vejdovsky) and the ascomycete *Cenococcum geophilum* Fr., could be responsible for the commonly reported detrimental effects of conifer crops on the biological activity of the soil, by reinforcing the effects of harsh climate and poor substrate quality in the absence of competitors (Meyer, 1964; Toutain, 1987; Ponge, 1990).

Despite minor changes in humus forms, aleppo pine exerts a marked influence on the biological functioning of the studied soils. This was ascertained by comparing plots increasingly dominated by pine. The gradient of development of the Oe horizon observed under the crown of adult pine trees in Sicily (Fig. 6) is probably at least partly due to the progressive development of the crown over the course of time, and thus to a longer-lasting influence of pine, from the time of its establishment, as the trunk is approached. In Navarre, edge effects have been observed near the border of the aleppo pine plantation, pointing to some improvement in litter decomposition in the understory due to changes in litter composition and microclimate (Collins and Pickett, 1987). The favorable influence of understory plant species on pine litter decomposition and humus form has

been reported (Tappeiner and Alm, 1975; Ponge and Prat, 1982; Emmer, 1994). This is probably due to a more diverse plant and decomposer community (Törne, 1978), but mechanisms by which pine litter is consumed at a higher rate in the presence of less recalcitrant litter are unknown.

The high level of soil biological activity observed under rosemary in the derelict scrubland of Navarre merits discussion. In Navarre, abundance of earthworm casts in the A horizon and rapid disappearance of litter (absence of an Oe horizon) are typical of humus profiles under rosemary bushes. The presence of the big soil-dwelling earthworm *S. campoii*, which has been observed to consume aerial as well as subterranean litter and mineral matter, is probably the reason for the rapid disappearance of rosemary litter. Under pine, the same earthworm species has been observed to consume pine needles and roots. It probably adapted its regime to changes in food resources following afforestation with pine, but the amount of pure pine litter reaching the ground at the inside of the plantation is probably higher than the amount populations of this endogeic species can consume each year. Before pine needles can be consumed by *S. campoii* they temporarily accumulate, forming the Oe horizon, a habitat favorable to fungal and arthropod activity (Ponge, 1991a; Torgersen et al., 1995). This adaptive behavior of soil animal and microbial communities is not unexpected since aleppo pine is a common inhabitant of present as well as past Mediterranean landscapes (Gindel, 1964; Naveh, 1971; Poli Marchese et al., 1988). Needle-consuming earthworms have been observed in places where conifer species are in their natural range (Bernier and Ponge, 1994; Bernier, 1998). In contrast, most inhibitory changes in soil biological activity have been observed in places where afforestation utilized exotic species (Hamilton, 1965). Nevertheless we can postulate that in Navarre, pine litter needs to be conditioned by microflora more than rosemary litter before being consumed or buried by native earthworms (Satchell and Lowe, 1967; Ponge, 1991b). This delay offers a permanent yet constantly renewed habitat for fungi and fungal-consuming fauna, whose contribution to the total biomass is known to increase under pine (Arpin et al., 1986a, 1986b; Arpin and Ponge, 1986).

In Sicily, we observed more uniformity among humus profiles. This could be due to the fact that pine litter dominates the forest floor everywhere, except under pistachio (Fig. 7). Personal observation suggests that pistachio leaves are more recalcitrant to comminution due to strong resistance to mechanical disruption; thus they share some mechanical features with pine needles. This can explain why, in contrast to Navarre, the Oe horizon was always present in Sicily. We observed a gradient in the development of the Oe horizon under pine crowns, pointing to the influence of pine on litter decomposition. The acidification of the soil in the vicinity of the trunk has been often attributed to stemflow (Mina, 1967; Bollen et al., 1968; Neite and Wittig, 1985), but this phenomenon occurs also in cases where stemflow is negligible (Beniamino et al., 1991). Bark deposi-

tion also contributes to soil acidification near the stem of pine (Zinke, 1962). We can postulate that a cumulative process of local soil impoverishment partly explains this phenomenon. As the tree grows, its crown enlarges. Thus, under an individual tree places far from the tree trunk have been influenced by pine much more recently than places located in the vicinity of the stem, which has undergone soil impoverishment from the time of pine establishment (Hamilton, 1965; Mettievier Meyer et al., 1986). Each time a wild fire destroys the forest and burns the accumulated litter, these effects disappear to appear again elsewhere during revegetation, which is always initiated with establishment of a new pine cohort.

ACKNOWLEDGMENTS

This work was supported by the European Commission DG XII-D (contract EV5V-CT94-0485). Many people are acknowledged for field assistance and accommodation, especially Pierre Arpin, Ignacio Armendariz, Rafael Escibano, Maria Teresa Vinciguerra, and staff technicians of host institutions.

REFERENCES

- Arpin, P., J.F. David, G.G. Guittonneau, G. Kilbertus, J.F. Ponge, and G. Vannier. 1986a. Influence du peuplement forestier sur la faune et la microflore du sol et des humus. I. Description des stations et étude de la faune du sol. *Rev. Ecol. Biol. Sol.* 23:89–118.
- Arpin, P., J.F. David, G.G. Guittonneau, G. Kilbertus, J.F. Ponge, and G. Vannier. 1986b. Influence du peuplement forestier sur la faune et la microflore du sol et des humus. II. Microbiologie et expériences au laboratoire. *Rev. Ecol. Biol. Sol.* 23:119–153.
- Arpin, P., and J.F. Ponge. 1986. Influence d'une implantation récente de pin sylvestre sur le comportement de la nématofaune du sol, par comparaison avec un peuplement feuillu pur et un peuplement mélangé. *Pedobiologia* 29:391–404.
- Babel, U. 1975. Micromorphology of soil organic matter. p. 369–473. *In* J.E. Gieseking (ed.) *Sol components. I. Organic components.* Springer Verlag, Berlin.
- Bal, L. 1970. Morphological investigations in two moder-humus profiles and the role of the soil fauna in their genesis. *Geoderma* 4:5–36.
- Bauzon, D., R. Van den Driessche, and Y. Dommergues. 1969. L'effet litère. I. Influence in situ des litières forestières sur quelques caractéristiques biologiques des sols. *Oecol. Plant.* 4:99–122.
- Beniamino, F., J.F. Ponge, and P. Arpin. 1991. Soil acidification under the crown of oak trees. I. Spatial distribution. *For. Ecol. Manage.* 40:221–232.
- Berg, B. 1984. Decomposition of moss litter in a mature Scots pine forest. *Pedobiologia* 26:301–308.
- Berg, B., K. Hannus, T. Popoff, and O. Theander. 1980. Chemical components of Scots pine needles and needle litter and inhibition of fungal species by extractives. p. 391–400. *In* *Structure and function of northern coniferous forests. An ecosystem study.* *Ecol. Bull.* 32:391–400.
- Berg, B., and B. Wessén. 1984. Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. *Pedobiologia* 26:285–298.
- Bernier, N. 1996. Altitudinal changes in humus form dynamics in a spruce forest at the montane level. *Plant Soil* 178:1–28.
- Bernier, N. 1998. Earthworm feeding activity and development of the humus profile. *Biol. Fertil. Soils* 26:215–223.
- Bernier, N., and J.F. Ponge. 1994. Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. *Soil Biol. Biochem.* 26:183–220.
- Bloomfield, C. 1953. A study of podzolization. I. The mobilization of iron and aluminium by Scots pine needles. *J. Soil Sci.* 4:5–16.
- Bollen, W.B., C.S. Chen, K.C. Lu, and R.F. Tarrant. 1968. Effect of stemflow precipitation on chemical and microbiological soil properties beneath a single alder tree. p. 149–156. *In* J.M. Trappe et al.

- (ed.) Biology of alder. Pacific Northwest Forest and Range Exp. Stn., Portland, OR.
- Bonneau, M. 1978. Conséquences pédologiques des enrésinements en forêt. C. R. Acad. Agric. Fr. 64:931-942.
- Brêthes, A., J.F. Brun, B. Jabiol, J.F. Ponge, and F. Toutain. 1995. Classification of forest humus forms: A French proposal. Ann. Sci. For. 52:535-546.
- Collins, B.S., and S.T.A. Pickett. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwood forest. Vegetatio 70:3-10.
- Elmi, S., and C. Babin. 1996. Histoire de la Terre. 3rd ed. Masson, Paris.
- Emmer, I.M. 1994. Humus form characteristics in relation to undergrowth vegetation in a *Pinus sylvestris* forest. Acta Oecol. 15: 677-687.
- Fisher, R.T. 1928. Soil changes and silviculture on the Harvard Forest. Ecology 9:6-11.
- Gindel, I. 1964. Seasonal fluctuations in soil moisture under the canopy of xerophytes and in open areas. Commonw. For. Rev. 43:219-234.
- Greenacre, M.J. 1984. Theory and applications of correspondence analysis. Academic Press, London.
- Hamilton, C.D. 1965. Changes in the soil under *Pinus radiata*. Aust. For. 29:275-289.
- Harris, L.D. 1988. Edge effects and conservation of biotic diversity. Conserv. Biol. 2:330-332.
- Kendrick, W.B., and A. Burges. 1962. Biological aspects of the decay of *Pinus silvestris* leaf litter. Nowa Hedw. 4:313-342 + 14 inlet plates.
- Kuiters, A.T. 1990. Role of phenolic substances from decomposing forest litter in plant-soil interactions. Acta Bot. Neerl. 39:329-348.
- Lainez, C., and R. Jordana. 1987. Contribución al conocimiento de los Oligoquetos (Oligochaeta, Lumbricidae) de Navarra. Ediciones Universidad de Navarra, Pamplona, Spain.
- Lawrey, J.D. 1986. Biological role of lichen substances. Bryologist 89:111-122.
- Lebart, L., A. Morineau, and J.P. Fénelon. 1979. Le traitement statistique des données. Dunod, Paris.
- McClurkin, D.C. 1970. Site rehabilitation under planted redcedar and pine. p. 339-345 In C.T. Youngberg and C.B. Davey (ed.) Tree growth and forest soils. Oregon State University Press, Corvallis.
- Macfadyen, A. 1962. Soil arthropod sampling. Adv. Ecol. Res. 1:1-34.
- Mettivier Meyer, H.J.B., J.W. Van Berghem, J. Sevink, and J.M. Verstraten. 1986. Studies on organic soil profiles. I. Methodology and its application to the Hulshorsterzand. p. 77-84. In J. Fanta (ed.) Forest dynamics research in Western and Central Europe. Pudoc, Wageningen, the Netherlands.
- Meyer, F.H. 1964. The role of the fungus *Cenococcum graniforme* (Sow.) Ferd. et Winge in the formation of mor. p. 23-31 + 1 inlet plate. In A. Jongerius (ed.) Soil micromorphology. Elsevier, Amsterdam, the Netherlands.
- Mina, V.N. 1967. Influence of stemflow on soil. Soviet Soil Sci. [1967]:1321-1329.
- Naveh, Z. 1971. The conservation of ecological diversity of Mediterranean ecosystems through ecological management. p. 605-622. In E. Duffey and A.S. Watt (ed.) The scientific management of animal and plant communities for conservation. Blackwell Scientific Publ., Oxford.
- Neite, H., and R. Wittig. 1985. Korrelation chemischer Bodenfaktoren mit der floristischen Zusammensetzung der Krautschicht im Stammfussbereich von Buchen. Acta Oecol. Oecol. Plant. 6:375-385.
- Ovington, J.D. 1953. Studies of the development of woodland conditions under different trees. I. Soils pH. J. Ecol. 41:13-34.
- Ovington, J.D. 1954. Studies of the development of woodland conditions under different trees. II. The forest floor. J. Ecol. 42:71-80.
- Poli Marchese, E., L. di Benedetto, and G. Maugeri. 1988. Successional pathways of Mediterranean evergreen vegetation on Sicily. Vegetatio 77:185-191.
- Ponge, J.F. 1984. Étude écologique d'un humus forestier par l'observation d'un petit volume, premiers résultats. I. La couche L₁ d'un moder sous pin sylvestre. Rev. Ecol. Biol. Sol. 21:161-187.
- Ponge, J.F. 1990. Ecological study of a forest humus by observing a small volume. I. Penetration of pine litter by mycorrhizal fungi. Eur. J. For. Pathol. 20:290-303.
- Ponge, J.F. 1991a. Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma 49:33-62.
- Ponge, J.F. 1991b. Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter. Plant Soil 138:99-113.
- Ponge, J.F. 1999. Horizons and humus forms in beech forests of the Belgian Ardennes. Soil Sci. Soc. Am. J. 63:1888-1901.
- Ponge, J.F., J. André, O. Zackrisson, N. Bernier, M.C. Nilsson, and C. Gallet. 1998. The forest regeneration puzzle: Biological mechanisms in humus layer and forest vegetation dynamics. BioScience 48:523-530.
- Ponge, J.F., P. Arpin, F. Sondag, and F. Delecour. 1997. Soil fauna and site assessment in beech stands of the Belgian Ardennes. Can. J. For. Res. 27:2053-2064.
- Ponge, J.F., and N. Bernier. 1995. Changes in humus form and forest dynamics in the French Northern Alps. p. 174-182. In D. Bellan et al. (ed.) Functioning and dynamics of natural and perturbed ecosystems. Lavoisier, Paris.
- Ponge, J.F., and L. Delhaye. 1995. The heterogeneity of humus profiles and earthworm communities in a virgin beech forest. Biol. Fertil. Soils 20:24-32.
- Ponge, J.F., and B. Prat. 1982. Les Collemboles, indicateurs du mode d'humification dans les peuplements résineux, feuillus et mélangés: Résultats obtenus en forêt d'Orléans. Rev. Ecol. Biol. Sol. 19: 237-250.
- Pons, A., and M. Thion. 1987. The role of fire from palaeoecological data. Ecol. Medit. 13:3-11.
- Reh, U., W. Kratz, G. Kraepelin, and C. Angehrn-Bettinazzi. 1990. Analysis of leaf and needle litter decomposition by differential scanning calorimetry and differential thermogravimetry. Biol. Fertil. Soils 9:188-191.
- Riha, S.J., B.R. James, G.P. Senesac, and E. Pallant. 1986. Spatial variability of soil pH and organic matter in forest plantations. Soil Sci. Soc. Am. J. 50:1347-1352.
- Robinson, R.K. 1972. The production by roots of *Calluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. J. Ecol. 60:219-224.
- Satchell, J.E., and D.G. Lowe. 1967. Selection of leaf litter by *Lumbricus terrestris*. p. 102-119. In O. Graff and J.E. Satchell (ed.) Progress in soil biology. Friedrich Vieweg and Sohn, Braunschweig, Germany.
- Tappeiner, J.C., and A.A. Alm. 1975. Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in Northern Minnesota. Ecology 56:1193-1200.
- Torgersen, C.E., J.A. Jones, A.R. Moldenke, and M. Le Master. 1995. The spatial heterogeneity of soil invertebrates and edaphic properties in an old growth forest stand in western Oregon. p. 225-236. In H.P. Collins et al. (ed.) The significance and regulation of soil biodiversity. Kluwer Academic Publ., Amsterdam, the Netherlands.
- Toutain, F. 1987. Les humus forestiers. Biodynamique et modes de fonctionnement. CRDP, Rennes, France.
- Van Berghem J.W., H.J.B. Mettievier Meyer, J. Sevink, and J.M. Verstraten. 1986. Studies on organic soil profiles. II. Succession of organic matter profiles in the Hulshorsterzand. p. 85-93 In J. Fanta (ed.) Forest dynamics research in Western and Central Europe. Pudoc Wageningen Press, Wageningen, the Netherlands.
- Van der Maarel, E. 1990. Ecotones and ecoclines are different. J. Veg. Sci. 1:135-138.
- von Törne, E. 1978. Experimenteller Nachweis zootischer Einflüsse auf den Stoffumsatz in einem Kiefernforst. Pedobiologia 18: 398-414.
- Zachariae, G. 1965. Spuren tierischer Tätigkeit im Boden des Buchenwaldes. Forstwiss. Forsch. 20:1-68.
- Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.